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TEMPORAL CONTROL IN RATS: ANALYSIS OF NONLOCALIZED EFFECTS FROM SHORT INTERFOOD INTERVALS

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The present experiment analyzed temporal control of postreinforcement pause duration during within-session changes in the criterion for reinforcement (interfood interval, IFI). Analysis of interval-by-interval changes in the pause revealed localized and nonlocalized effects from short intervals that caused specific changes in performance. In Phase 1, rats were presented with five consecutive 15-s IFIs intercalated into a series of 60-s IFIs. The 15-s set decreased the pause in adjacent and more remote 60-s intervals. In Phase 2, two sets of 15-s intervals were intercalated. The spacing between the two sets varied so that 0, 5, 10, or 15 60-s IFIs separated the sets. The postreinforcement pause tracked all changes in the IFI duration, and the localized effect from a short set extended beyond the next interval to the next few 60-s IFIs. Effects from one set, however, did not combine with a second set: Changes in the pause after two sets were the same regardless of the spacing between sets.

Key words: temporal control, dynamics, nonlocalized effects, interfood interval, postreinforcement pause, lever press, rats

Animals exposed to periodic reinforcement frequently show behavioral sensitivity to the duration of time between successive reinforcers. An example of this behavioral effect, called *temporal control,* is performance on fixed-interval (FI) reinforcement schedules in which a reinforcer is given for the first response after a fixed amount of time has elapsed since delivery of the preceding reinforcer. The standard method typically involves exposing animals to a single FI value for many trials and sessions. The end result is a distinctive pattern of responding between successive reinforcers (interfood interval, IFI): A postreinforcement pause (PRP) is followed by either a gradual acceleration in responding as the programmed time to the next reinforcer nears or a break-and-run pattern (e.g., Ferster & Skinner, 1957; Schneider, 1969).

Recent studies have investigated temporal control under less routine situations. Instead of giving animals many sessions of exposure to a single FI value, they are presented with frequent changes in the time to reinforcement. The changes usually occur within a session, on a trial-to-trial basis, and are unsignaled (e.g., Higa, Wynne, & Staddon, 1991; Wynne & Staddon, 1988; Wynne, Staddon, & Delius, 1996). In these studies, the primary measure of temporal control is based on the well-established finding that PRP duration is directly related to the FI requirement (e.g., Zeiler & Powell, 1994; see Richelle & Lejeune, 1980, for a review of other dependent measures of temporal control). As with standard procedures, animals show proportional changes in their PRP duration as a function of changes in the IFI duration. A notable finding is that an unsignaled change in the IFI duration often has an immediate effect after a single interval (e.g., Higa et al., 1991; Wynne & Staddon, 1988). The rapid ''tracking'' of changes in the criterion to reinforcement has also been shown when the requirement varies on a daily basis (e.g., Lejeune, Ferrara, Simons, & Wearden, 1997; Wynne & Staddon, 1992).

Work on timing dynamics has also revealed that performance—under certain conditions—depends on more than the just-preceding interval. For example, when presented an unsignaled increase in the IFI duration (e.g., from 15 to 45 s), rats and pigeons show an initial rapid increase in their PRP duration

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after the first long interval, but the PRP continues to increase across several subsequent intervals (e.g., see Higa, 1997; Higa, Thaw, & Staddon, 1993). The gradual increase indicates that the PRP was affected by the shorter pretransition intervals. If the PRP under longer intervals did not depend on the preceding shorter intervals, then the PRP would have increased immediately after the first long interval and remained long across subsequent intervals. Hence, effects from the shorter (pretransition) intervals appeared to combine and extend beyond the next adjacent interval, to produce ''nonlocalized'' changes on temporal performance in upcoming intervals.

Nonlocalized effects from short intervals have also been reported when there is a temporary transition in the IFI duration. In one study (Higa, 1996), pigeons were presented with eight 5-s intervals intercalated in a series of 15-s intervals. (The 5-s intervals occurred in succession and began at an unpredictable point within a session.) Pigeons' PRP duration decreased substantially after the first short interval and remained short during the 5-s IFIs. Moreover, when IFIs returned to 15 s, PRPs were shorter than those observed in 15-s IFIs preceding the transition. In other words, PRP duration was reduced and was slow to recover to pretransition levels. Separating each 5-s IFI with four 15-s IFIs, however, prevented the slow recovery of PRP duration. Hence, PRP is not only sensitive to a recent change in IFI duration, but it is also dependent—in a systematic way—on more remote IFIs.

These results indicate that an important question to ask is how temporal control depends on nonlocalized factors generated by intervals within a series. Given that a set of consecutive short IFIs shortens the PRP in longer IFIs, it is possible that a series with repeated downward changes in IFI duration may cause an overall decrease in PRP duration in all intervals. The dynamics associated with transitions in the IFI duration may, therefore, explain some experimental data in which PRP duration does not change systematically with frequent changes in the IFI duration. For instance, PRP duration remains about the same across intervals under variable-interval (VI) schedules and some simple cyclic, square wave reinforcement schedules (e.g., a repeating cycle of 12 FI 60-s 4 FI 180-s intervals, Staddon, 1967). Finally, an intermediate case of temporal tracking also indicates that effects from prior intervals can accumulate and combine as training progresses to alter temporal control. Pigeons' PRPs initially tracked a repeating series of intervals (15, 45, 15, 5 s), but tracking of the IFIs by the PRP degraded with training so that PRP duration was approximately the same in all intervals—shorter, overall, than a baseline condition in which all IFIs were 15 s (Higa et al., 1993).

The present study was designed to investigate, in two phases, the effects on the PRP of local and more distant intervals within a series of intervals. To study these effects, we presented rats with two sets of short IFIs that were intercalated into a series of longer intervals and measured the PRP in all intervals. The spacing between sets was varied across conditions. A single set of short intervals by themselves has already been shown to decrease the PRP in subsequent IFIs (e.g., Higa, 1996). Hence, to the extent that the impact of one short IFI set combines with that of a second short set, the spacing between two sets of short IFIs should differentially affect the PRP duration in more remote (subsequent) intervals.

In Phase 1, we first established that a sequence of five consecutive 15-s IFIs shortens the PRP duration in subsequent 60-s intervals. The procedure was similar to that from Higa's (1996) study; however, there were a few differences. We used different IFI durations, rats instead of pigeons, and FI schedules instead of a response-initiated-delay (RID) schedule (equivalent to a conjunctive fixed-ratio 1 fixed-time reinforcement schedule). We showed that five 15-s intervals did produce significant nonlocalized decreases in the PRP duration in adjacent longer intervals. In Phase 2 we evaluated the effects of separating two sets of 15-s IFIs in five conditions. Of interest were changes in PRP duration with respect to changes in the spacing between sets of short intervals, including the recovery pattern of PRP duration following each set. Specifically, if there are cumulative effects from sets of short IFIs, (a) the PRP should be shorter following a closely spaced set of short intervals, and (b) the recovery of PRP duration (to levels observed before short

intervals were introduced) should be slower after a second set of short intervals than after the first set. The recovery should be slower in that PRP should be shorter in many more ensuing intervals.

METHOD

Subjects

Five adult male Sprague-Dawley rats (996, 1096, 1196, 1296, and 1396) served as subjects. All subjects already had experience obtaining food reinforcers by pressing levers and had limited experience on fixed-ratio reinforcement schedules, but none had experience on a temporal discrimination task. We studied the rats 5 to 6 days a week and gave them supplementary food at the end of each day to maintain them at approximately 80% of their free-feeding body weights. The rats had free access to water in their individual home cages and were housed in a colony with a 14:10 hr light/dark cycle. The experiment took place during the light part of the cycle.

Apparatus

We conducted the experiment in five operant conditioning chambers. Each chamber was approximately 27 cm wide, 31 cm deep, and 20 cm high. Mounted on the front panel of each chamber was a flat lever, 5 cm long and 2 cm wide, located 3.5 cm above the floor and 8 cm from the right wall. Mounted directly above the lever was a lamp approximately 1.5 cm in diameter. A 3-cm aperture, 8 cm to the left of the lever, provided access to liquid reinforcers. A houselight, mounted in the center of the ceiling, illuminated the chamber. The chamber was enclosed in a sound-attenuating enclosure, which also contained a fan to mask extraneous noise. Five IBM-compatible computers and a complied program written in BASIC controlled the experimental events and recorded all lever presses.

Procedure

For all experimental conditions a session began with delivery of a reinforcer (marking the start of a session and the first IFI) followed by 50 IFIs programmed according to an FI reinforcement schedule. A reinforcer was delivered for the first response that occurred after a fixed amount of time had elapsed since the preceding reinforcer delivery. The houselight remained on throughout a session, and the light above the lever was always lit except during the delivery of the reinforcer. Reinforcement consisted of 3-s access to a 0.10-cc dipper cup holding diluted condensed milk (50% condensed milk and 50% water by volume).

Phase 1. We exposed all subjects to a baseline and an experimental condition. During baseline, all intervals were programmed to be the same duration, 60 s. After five sessions of baseline, subjects were trained on a one-set condition. For this condition, we intercalated (programmed) five consecutive 15-s IFIs into the series of 60-s IFIs (see Figure 1), holding constant the total number of IFIs per session across baseline and the experimental condition. We randomized the location of the 15-s set across sessions, with one constraint: At least 10 60-s IFIs had to occur before the first 15-s IFI and after the last 15-s IFI. We gave each subject 10 sessions of training on the one-set condition.

Phase 2. Following Phase 1, we gave subjects training on two sets of five 15-s IFIs. Either 0, 5, 10, or 15 60-s IFIs were programmed to occur between the last 15-s interval of the first set and the first 15-s interval of the second set, holding constant the total number of IFIs per session (to 50). Figure 1 presents a diagram of the different input sequences of IFIs. As before, the location of the short sets of IFIs was randomized across sessions, with the constraint that at least 10 60-s IFIs had to occur before the start of the first set and after the second set.

Subjects were given five sessions of training on each condition—two sets (0), two sets (5), two sets (10), or two sets (15)—and the order of conditions varied across sessions, such that each condition occurred once in a block of four sessions (subjects received the same randomized sequence of conditions). In terms of the spacing between the two sets, the order was 10, 5, 0, 15, 5, 10, 15, 0, 15, 0, 5, 10, 0, 15, 5, 10, 0, 5, 10, 15. We varied the conditions daily, instead of conducting massed training sessions, to attenuate the likelihood that rats would learn to anticipate the first short interval and base their responses on events other than the IFI duration. This possibility was potentially high for the two-set

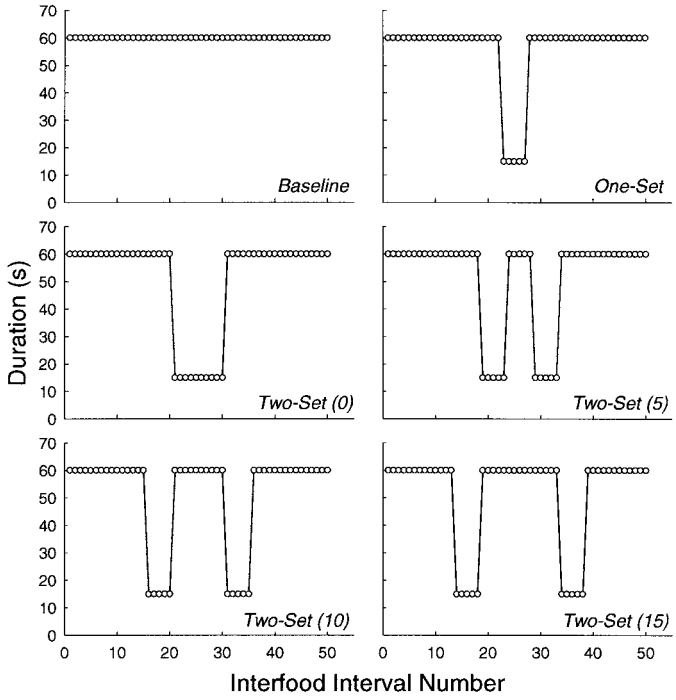

Fig. 1. Diagram of the different input series (conditions) used in Phases 1 and 2.

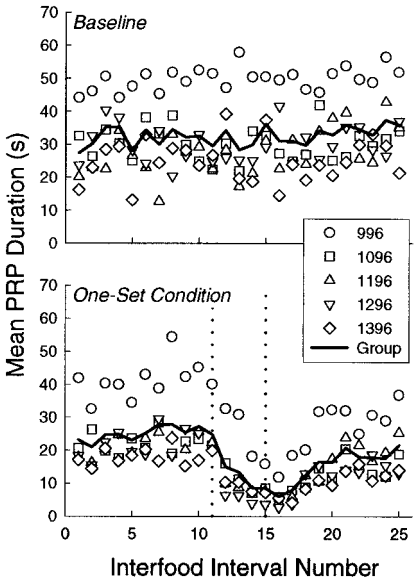

Fig. 2. Results from Phase 1. Mean postreinforcement pause (PRP) duration for individual subjects (open symbols) and the group average (solid lines) during a subset of intervals from the first baseline and the one-set condition (see text for averaging method). The dashed vertical line for the one-set condition marks the first and last 15-s IFIs. Surrounding IFIs were 60 s in duration.

(15) condition, in which the constraints described earlier (e.g., requiring at least 10 60-s intervals around the short sets) limited the variation in the location of the first set of short intervals. At the end of the rotation through the two-set conditions, we exposed the rats to another baseline condition for 10 sessions.

RESULTS

Phase 1

Figure 2 (top panel) presents the results from the first baseline condition. For individual subjects, performance during baseline was determined by randomly selecting an interval in which a short IFI would have been programmed to occur in the one-set condition. PRPs from that IFI, the next four IFIs, and the 10 surrounding IFIs were selected from each session (for a total of 25 intervals), and then an average was calculated. Hence, the PRP durations from a comparable number and location of IFIs were selected for comparison with the results from the one-set condition. The results from the baseline condition indicate that there were individual dif-

Table 1

Results of repeated measures analyses of variance applied to the PRP duration in the intervals presented in the figures.

Condition	Factor	*df*	Results
First baseline	Interfood interval number (IFI)	24, 96	1.26
Phase 1 (one set)	Transition	1, 4	50.81**
	IFI	4, 16	6.59**
	Transition × IFI	4, 16	9.57**
	Adjacent	1, 4	64.16***
	IFI	4, 16	4.18*
	Adjacent × IFI	4, 16	3.95*
	Distant	1, 4	14.985*
	IFI	4, 16	0.62
	Distant × IFI	4, 16	1.12
Phase 2 (two sets)	Transition	1, 4	14.82*
First short set	IFI	4, 16	9.34***
	Spacing	3, 12	0.76
	Transition × IFI	4, 16	8.20***
	Transition × Spacing	3, 12	4.40*
	IFI × Spacing	12, 48	0.63
	Transition × IFI × Spacing	12, 48	0.59
Second short set	Transition	1, 4	12.42**
	IFI	4, 16	5.26**
	Spacing	2, 8	4.04
	Transition × IFI	4, 16	11.80***
	Transition × Spacing	2, 8	2.71
	IFI × Spacing	8, 32	2.43*
	Transition × IFI × Spacing	8, 32	1.70
Recovery	Condition	3, 12	2.49
First short set	IFI	4, 16	10.62***
	Condition × IFI	12, 48	1.17
Second short set	Condition	3, 12	2.02
	IFI	4, 16	10.40***
	Condition × IFI	12, 48	0.91
Second baseline	IFI	24, 96	2.82***

* $p < .05$, ** $p < .01$, *** $p < .001$.

ferences in performance. For example, the PRP for 1 subject (996) was generally longer than that for the other rats. A one-way repeated measures analysis of variance (ANOVA) on PRP duration as a function of the ordinal number of the IFI was not significant. The results from all statistical tests are presented in Table 1. Throughout this study, an effect was considered to be significant when $p \leq .05$.

For the one-set condition, we extracted the PRP from the 15-s intervals and the 10 preceding and following intervals (for a total of 25 intervals) and then calculated mean PRP for these intervals, for all sessions of training. The results are shown in Figure 2 (bottom panel). Several effects are evident in the results. First, PRP duration was significantly shorter, overall, in the 15-s intervals than in the just-preceding five 60-s intervals (Table 1, main effect of transition). Note that because the first 15-s IFI is unsignaled, PRP in this interval should be approximately the same as that in preceding intervals.

In addition to an immediate decrease in PRP duration, a set of 15-s IFIs also shortened the PRP duration in the 60-s intervals immediately following the short set and in more remote intervals. Specifically, there was a significant decrease in PRP in the five IFIs before versus after the short set (Table 1, adjacent). In addition, PRPs from the last five IFIs shown in Figure 2 were consistently shorter than those in the five IFIs before the short set (Table 1, distant).

Phase 2

The results from the two-set conditions are given in Figure 3. We calculated mean PRP as before, and the dashed vertical lines mark the start and end of each set of 15-s intervals. Several effects are evident in the pattern of

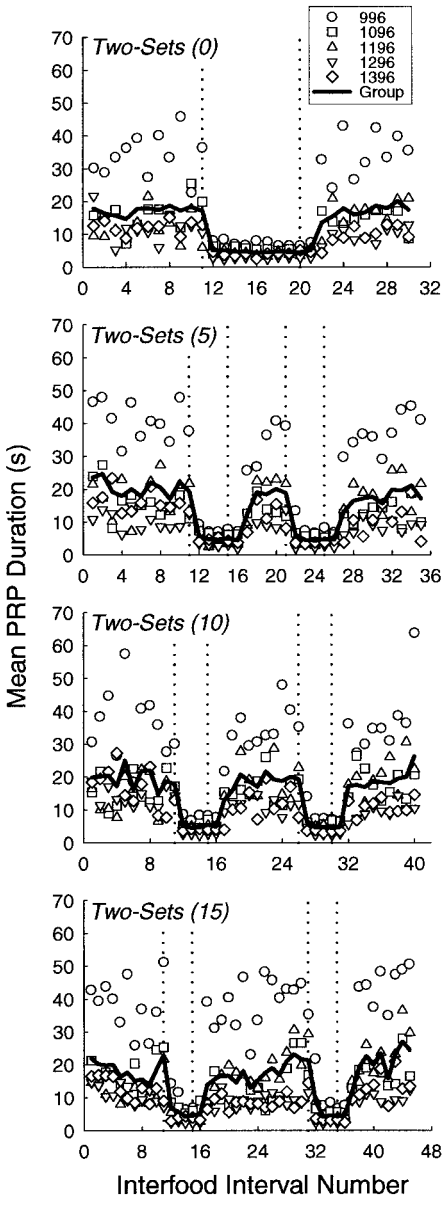

Fig. 3. Results from Phase 2. Data are the mean post-reinforcement pause (PRP) duration from the two sets of 15-s IFIs, the IFIs between the sets, and the 10 IFIs that occurred before the first and after the last 15-s IFI. The results for individual subjects (open symbols) and the group mean (solid line) are given. See text for averaging method. The dashed vertical lines mark the start and end of each set of 15-s IFIs.

responding under the different conditions. First, what happened with the first short set? PRP shortened after the initial 15-s interval and either decreased slightly [e.g., two sets (15)] or remained at a steady level across the shorter IFIs [e.g., two sets (0)]. A three-way repeated measures ANOVA (Table 1, with IFI, transition, and spacing as factors) confirmed that the difference in PRP duration during the first short set and the five just-preceding (60-s) intervals was statistically significant. Although overall PRP levels did not depend on the spacing of the two short sets of intervals, there was a significant interaction effect between the PRP (before and after a transition) and on the spacing between sets (Table 1, Transition × Spacing).

What was the effect of a second set of 15-s IFIs on temporal control? As with the first short set, a second set caused a significant decrease in PRP duration. For the two-set (0) condition (in which no 60-s IFIs interrupted the sets), the PRP remained short, at approximately the same level as that seen in the first short set of intervals. For the remaining conditions, PRP decreased significantly from approximately 20 to 4 s. A three-way repeated measures ANOVA on PRPs from the second short set and the just-preceding five IFIs [conducted on all but the two-set (0) condition] confirmed the differences seen in Figure 3. However, PRPs in these intervals did not differ across the two-set conditions (see Table 1).

To study, more carefully, the recovery after each short set, we plotted in Figure 4 only the PRPs from the five intervals following each set. The PRP pattern of recovery after one set of short intervals was approximately the same across conditions, with the exception of the two-set (0) condition (the PRPs for this condition are from another set of 15-s intervals that immediately followed the first set). Overall, there was a gradual increase in PRP duration for the mean function, which continued through the third interval. The functions for the individuals were more variable but were, in the main, consistent with the mean function. The effect was significant across intervals, but there were no significant differences across the one-set and two-set (5), two-set (10), and two-set (15) conditions (Table 1, main effect of condition, first short set). Recovery after a second set of short intervals was also gradual, and there were no consistent differences across conditions (Table 1, main effect of condition, second short set).

The results from the final baseline condition are given in Figure 5. PRPs for each sub-

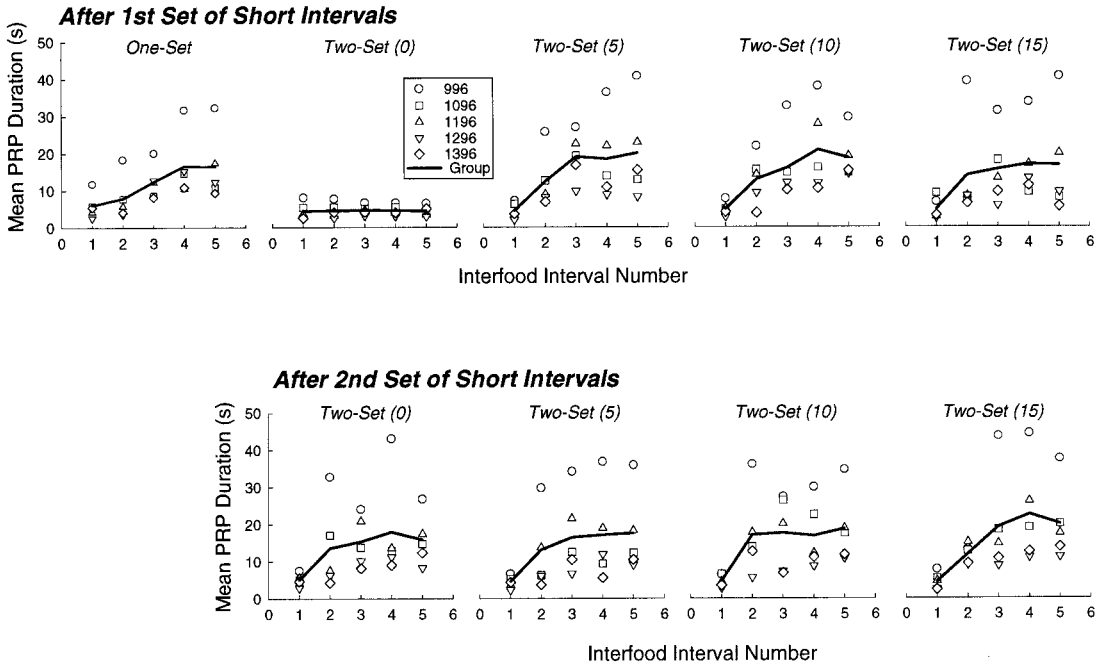

Fig. 4. Recovery. Presented are the postreinforcement pauses (PRP) from the first five IFIs after each set short set of intervals. The results for individual subjects (open symbols) and the group mean (solid line) are given. Note that for the two-set (0) condition, the PRPs are from the second short set. For this condition, no 60-s IFIs interrupted the sets.

ject were determined as was done for the first baseline condition. The PRPs appear shorter, overall, than those during the first baseline, and there is a general increase across the intervals. A one-way repeated measures ANOVA on PRP from these intervals was significant.

DISCUSSION

The present study investigated the role of nonlocalized effects (from a set of short IFIs) on temporal control in rats. In Phase 1, the goal was to establish that PRP was sensitive to

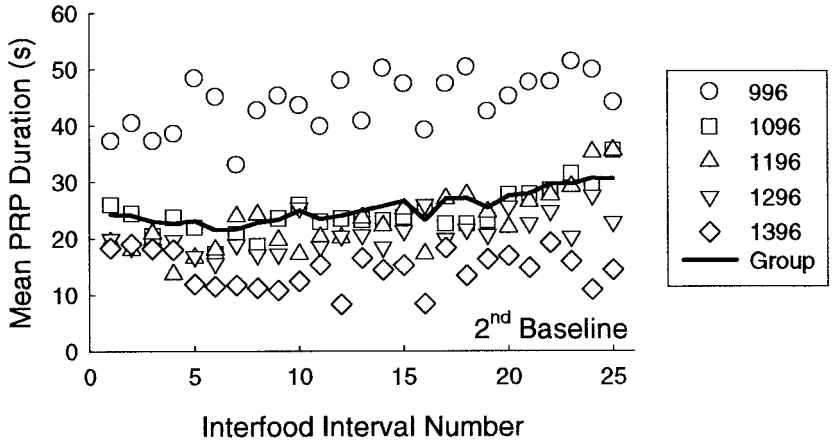

Fig. 5. Mean PRP duration for individual subjects (open symbols) and the group (solid line) during the second baseline condition.

an unsignaled temporary change in the FI requirement (from 60 to 15 s and back to 60 s) and that the PRP in subsequent longer intervals was also shortened. As in previous studies with pigeons (e.g., Higa et al., 1991; Wynne & Staddon, 1988), the PRPs of our rats tended to track the input sequence of IFIs by decreasing after the first short interval. When the criterion for reinforcement returned to 60 s, PRP increased, but somewhat gradually across several intervals. This pattern of PRP during 60-s intervals that were preceded by 15-s intervals indicates that a set of relatively shorter intervals had effects that persisted over a series of subsequent intervals. Such nonlocalized changes in PRP duration are consistent with the results of previous research with rats (Higa, 1997) and pigeons (Higa, 1996) that used different IFI values and different reinforcement schedules (e.g., RID instead of FI schedules).

In Phase 2 the method and results from Phase 1 were used to study how temporal control depended on differently spaced sets of 15-s intervals. As in Phase 1, we observed nonlocalized changes in PRP duration after each set. However, we did not find evidence that the effects from one set combined with another: There were no consistent differences in the pattern of PRPs during or following the last set in each condition. If the nonlocalized effects from one set did combine with those from the other set, then the PRP should have been shorter and slower to recover with a smaller spacing between sets. The present study clearly indicates that a set of consecutive short IFIs affected subsequent PRP in neighboring longer IFIs. However, these effects did not combine or accumulate to alter future PRPs systematically.

The results from the one-set and two-set (0) conditions were especially surprising in light of previous research with pigeons, which showed that the recovery of PRP duration in long intervals (45 s) was slower after eight than after two successive short intervals (15 s; e.g., Higa, 1996). We found no consistent difference in the recovery pattern. One difference between these studies is that we rotated the different two-set conditions across sessions, instead of presenting each condition in a massed form. Previous studies have revealed different patterns in tracking when conditions alternate daily. For example, under massed conditions (i.e., when a condition was in effect for several consecutive sessions), pigeons show little difference in tracking a sinusoidal sequence of IFIs as a function of whether the intervals were short (5 to 15 s) or long (30 to 90 s). For both ranges, the average pause in each interval was proportional to the previous IFI duration. When the short and long conditions were alternated between sessions, tracking the long series was more impaired than the short, such that the correlation between pause in one interval and the previous IFI duration was reduced (Higa et al., 1991).

Another possible explanation is that our rats may have simply learned to anticipate a period of time in a session when the IFIs would increase in duration and remain long—that is, after the last short set. The same pattern of recovery in the one-set and two-set conditions may simply indicate the anticipation of the return to a longer IFI value. The overall increase in PRP duration in the second baseline condition suggests this may indeed have occurred. Alternatively, it is possible that the increase in PRP during the final baseline condition is a kind of *within-session* effect (e.g., McSweeney, Hatfield, & Allen, 1990). Recent studies on within-session changes in response rate during variable-interval reinforcement schedules demonstrate systematic changes in responding as a function of time in a session. A typical pattern is an initial increase then decrease in the rate of responding as a session progresses (e.g., McSweeney & Hinson, 1992). Our results with PRP duration and FI 60-s reinforcement schedules may reflect a similar process. However, we did not find evidence for systematic changes in PRP duration in the first baseline condition. Furthermore, because we varied the location of a short set across sessions, it is unlikely that our main effects are the sole result of a process in which the PRP changes across a session when IFI duration is constant.

To conclude, a set of short intervals, intercalated into a series of longer intervals, produced both local and nonlocalized changes in temporal control. However, the nonlocalized effects from a set of short intervals—that is, a shortening of the PRP duration in neighboring longer IFIs—did not combine across sets to differentially affect performance. What kind of mechanism underlies these tim-

ing dynamics? With a few exceptions (e.g., Wynne et al., 1996), most theories have focused on explaining the steady-state properties of timing (e.g., Fetterman & Killeen, 1991; Gibbon, 1977; Gibbon, Church, & Meck, 1984; Killeen & Fetterman, 1988). The present results suggest that understanding the dynamics of temporal control may contribute to (and complement) steady-state approaches, and may shed light on a more general model of timing.

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